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16. Abstract

A comparative study of the projection of vestibular afferents to the postcruciate dimple and to the primary vestibular area is given. The results, obtained with three different recording methods, revealed a localized site of relatively early vestibular response in the deep cruciate sulcus, and indicated the primary nature of the vestibular projection to the suprasylvian cortex and the abundance of vestibulo-somatic convergence in the cortical areas studied.

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1. Introduction   <u>/60</u>*

During the past few years, several electrophysiological studies
have been concerned with ascending vestibular projections, es-
pecially projections to the cerebral cortex.

A large number of macrophysiological studies have approached
this subject in the cat. The vestibular stimulation consisted of
stimulation delivered at the vestibular nuclei [18], stimulation
of the vestibular nerve [21, 22, 30], or stimulation of one of the
nerves emanating from the ampullae of the anterior and horizontal
semicircular canals or from the utriculus. This technique,
developed by Andersson and Gernandt [1], permitting very localized
and very precise stimulation of the labyrinth, was used by
Milojevic and Saint-Laurent [23], Landgren et al. [17], and
Sans et al. [27]. The results obtained with the use of these dif-
ferent methods have revealed an area of primarily contralateral
vestibular projections to the cerebral cortex of the cat, located
on either side of the anterior suprasylvian sulcus. Due to the
constancy of the responses produced in this cortical area and their
relatively short and closely uniform latency period, it may be
assumed that labyrinthine projections in this area of the cortex
are primary in nature.

Similar research performed on the monkey by Fredrickson et   <u>/61</u>
al. [5] has shown that stimulation of the vestibular nerve also

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* Numbers in the margin indicate pagination in the foreign text.

induces a response of primary type in a cortical area restricted to the posterior part of the posterior central gyrus, at the base of the intraparietal sulcus. The fact that this area is located between the first and second somatic areas suggests that this area is a homolog of the labyrinthine area revealed in the cat.

There has been a great deal of microphysiological research on this subject. An initial approach by Jung et al. [13] showed that polarization of the labyrinth influences the activity of the neurons of the anterior suprasylvian area. In a more recent study using stimulation of the nerves emanating from the ampullae of the semicircular canals, Landgren et al. [17] have observed reponses with a short latency period induced by this stimulation in the neurons of this same cortical area.

At the same time, other studies have suggested that labyrinthine stimulation influences the motor output through an ascending path passing through the motor cortex. In this connection we might mention the work of Megirian and Troth [20] and Megirian and Manning [19], who recorded a pyramidal discharge following vestibular stimulation, or again, the results of the experiments performed by Morrison and Pompeiano [24]. The latter investigators have shown that there is no longer any phase increase in the pyramidal discharge during paradoxical sleep after lesion of the vestibular nuclei. Finally, the research of Kornhuber and da Fonseca [15], and more recently, that of Boisacq-Schepens and Hanus [2] have revealed the vestibulosomatic nature of the motor cortex. The latter study has shown that vestibular stimulation under the effects of chloralose produces a positive macroresponse in the pericruciate cortical region after a latency period of 10 to 15 msec, and that, on a unit level, 40% of the neurons in this cortical area receive vestibular influxes after an average latency period of 26 msec.

However, the importance of labyrinthine projections to the motor cortex of the cat has increased since Sans et al. [27] and Boisacq-Schepens and Hanus [2] used monopolar surface macro-electrodes to record a wave occurring after a brief latency period (5 to 6 msec) with a low stimulation threshold, centered on the postcruciate depression. A similar wave was obtained in the monkey in front of the inferior part of the central sulcus by stimulation of the vestibular nerve [5]; this response does not appear very stable, however.

The significance of these results and the limited amount of /62 microphysiological research dealing with cortical vestibular projection led us to pursue this problem and to use microelectrodes and concentric bipolar macroelectrodes to study the reponses of the cat in the anterior suprasylvian area and the postcruciate depression during electrical stimulation of the nerve emanating from the ampulla of the horizontal semicircular canal. Preliminary discussions of this research have been published [3, 25].

Methods

The experiments were performed on 30 cats anesthetized with α-chloralose (60 mg/kg IV); the animals were immobilized with curare and artificial respiration was used. The partial CO_2 pressure in the expired air was continuously monitored and was kept in the vicinity of 3.8%.

Stimulation

The animals were subjected to: (1) somatic stimulation consisting of simple electric shocks (5 to 10 V; 0.5 msec) delivered by a pair of hypodermic needles placed under the skin at the end of each paw;

(2) vestibular stimulation consisting of electrical stimulation of the nerves emanating from the ampulla of the horizontal semicircular canal, using the method developed by Andersson and Gernardt [1] and modified by Dumont-Tyc and Dell [4] (for details, see [2]).

Recording

In an initial series of experiments, the responses of the interior suprasylvian area and the postcruciate depression to these types of stimulation were recorded, either by monopolar surface recording using a pair of silver balls with the neutral ball placed under the temporal muscle, or by transcortical bipolar recording using concentric macroelectrodes. The connections were such that a variation in positive potential at the tip of the electrode resulted in a downward deflection of the oscillographic pattern.

In a second series of experiments, unit recordings were made using extracellular micropipettes filled with a pontamine staining solution and whose measured resistance in the filling solution was on the order of 4 MΩ [8]. The responses were observed on an oscilloscope and, in some cases, were filmed and stored on magnetic tape for later analysis.

It should be noted that in all cases the recordings were made in the part of the cerebral cortex contralateral to the vestibular stimulation. In this type of system, the ipsilateral or contralateral somatic afferents are designated in relation to the part of the cerebral cortex recorded.

Histological Marking

A marking technique derived from that described by Green et al. [9] was used for accurate pinpointing of the positions of the

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macroelectrode tip in the nerve tissue. At the end of the descent,
a 50 µA current was passed through the neutral electrode for
2 min, producing an iron deposit in the nerve substance. At the
end of the experiment, the brain of the animal was perfused with
a solution of 20% formol and potassium ferri-ferrocyanide,
staining the deposited iron ions. In this way, it is easy to
mark a blue spot on 100 µm sections prepared by freezing and   <u>/63</u>
stained by the Nissl method. Marking of the terminal point of
descent of the microelectrode by the injection of stain [8] and
pinpointing of its point of penetration permitted precise recon-
struction of each descent performed.

Results

I. Macrophysiological Results

Monopolar surface recordings (limited to the cerebral cortex
contralateral to the vestibular stimulation) made it possible for
us to confirm the presence of an extremely stable, short latency
period (4 to 5 msec) response in the anterior suprasylvian area.
This response occurred at a very low threshold of stimulation of
the ampullar nerve (minimum stimulation producing a response in
the primary vestibular nuclei: 1 to 2 V, 0.2 msec): this response
occurred in the form of a small brief positive wave. We were
able to record a lower amplitude wave in the postcruciate de-
pression, but the threshold and the latency period for this wave
were the same as for the wave recorded in the suprasylvian area
(Fig. 1). It should be recalled that the sigmoid, coronary and
lateral gyri also respond to vestibular stimulation; however, these
responses occur at a slightly higher stimulation threshold and
after a longer period of latency (10 to 15 msec).   This delayed
component may also be recorded in the suprasylvian and post-
cruciate regions after the early positive wave, and it undergoes
the depressant interaction described in the following paragraph.

The effects of somatic conditioning stimulation on the response to the vestibular stimulation test were examined in the suprasylvian area and the postcruciate depression. In these two cortical regions, it was observed that the first component of the wave was present constantly, no matter what the period between two stimulations might be, while the second component disappeared completely for waiting periods of up to 100 msec; it subsequently showed a gradual recovery which became complete when the two stimulations were separated by a period of 300 msec. The persistence of the early component of the response indicates that this part of the response is specific. This early component of the response will be the only one considered in the following discussion.

Another finding was made during our monopolar surface derivation tests. This concerned the possible recording at point 2 /64 of a response whose configuration and latency period was identical to those of the responses recorded at points 1 and 3 (Fig. 1) (that is, at the site located between the primary vestibular area, point 3, and the postcruciate depression, point 1).

The sum total of the results obtained with monopolar surface recording offered no information on the problem of the origin of the response recorded in the postcruciate depression. It was yet to be determined whether this consisted of long-distance recording of the response produced in the anterior suprasylvian area or a response originating in the neurons of the motor cortex. To /65 shed some light on this problem, concentric bipolar macroelectrodes were used to perform systematic descents into the anterior suprasylvian area and the area centered on the postcruciate depression. No response to vestibular stimulation was recorded in the postcruciate depression with the use of bipolar surface derivation, nor was there any response in the superficial cortical layers. A focal negative wave occurred when the recording electrode penetrated into the cortical layer bordering on the lower bank
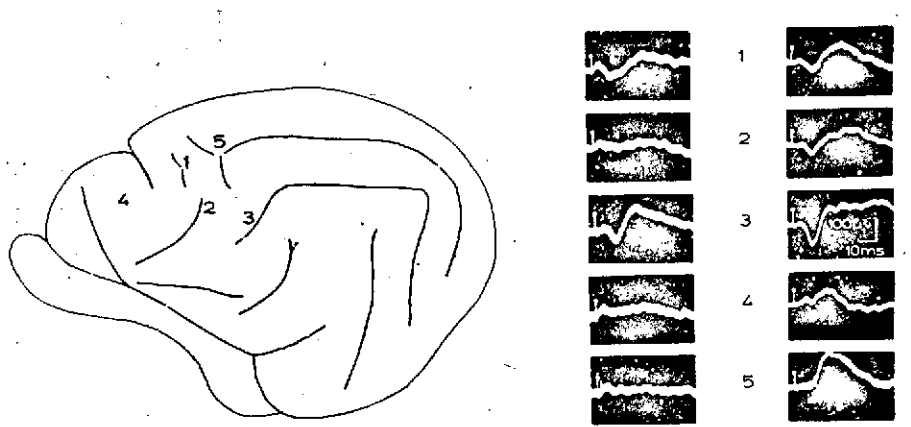
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Fig. 1. Examples of monopolar surface recordings of
cortical macroresponses produced by stimulation of the
nerve emanating from the ampulla of the contralateral
horizontal semicircular canal; chloralosed cats. The
diagram on the left shows the recording sites:
1. depression of the postcruciate cortex.
2. the upper part of the coronary sulcus.
3. anterior suprasylvian gyrus or primary vestibular
   area.
4. the precruciate cortex.
5. the lateral gyrus.
On the right are photographic examples of the responses
recorded: in one animal, with a stimulation threshold of
1.5 V (left-hand column); in another animal, with a
stimulation threshold of 2.5 V (right-hand column). In
the right-hand column, the brief latency period, low
threshold response for the recordings made at position
1 (postcruciate dimple), position 3 vestibular
area) and also position 2 (coronary sulcus) should be
noted. In the same animal, a more delayed response with
a higher threshold was observed at the other recording
sites.

of the internal part of the cruciate sulcus, that is during

insertions performed at anterior planes 22 to 24 and at lateral

planes 4 to 8 (Fig. 2). This response was in the form of a

relatively prolonged wave occurring after a latency period of   /66

6-7 msec and disappearing at a repetitive stimulation frequency of

3/sec. There was little difference between this response and the

response recorded in the deep anterior suprasylvian area using the

same method. In this region, a negative wave occured after a

a constant latency period of 4 msec; this wave might follow a

repetitive stimulation frequency of 5/sec. This wave may be re-
corded over a height including both banks of the suprasylvian
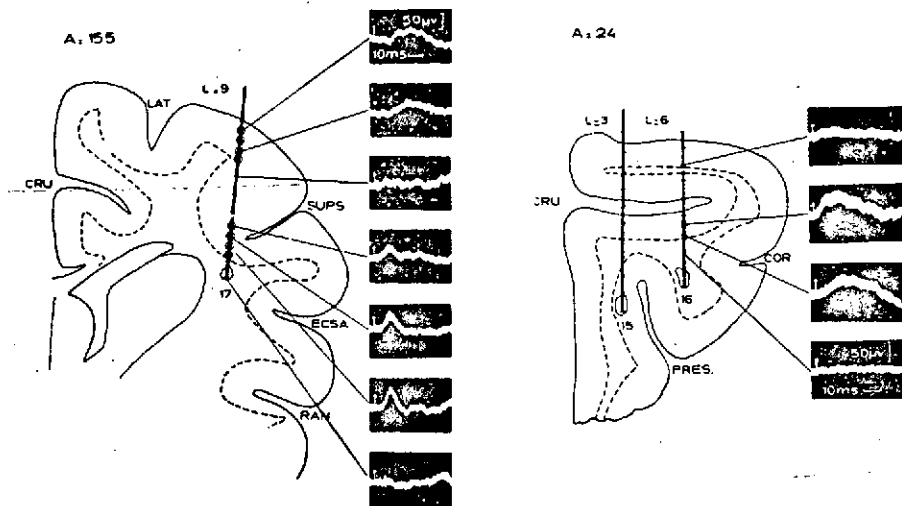sulcus in anterior planes 14 to 17 (Fig. 2).

Fig. 2. Examples of descents performed by means of
concentric bipolar macroelectrodes, entering frontal
plane 15.5 of the suprasylvian cortex on the left, and
frontal plane 24.0 of the postcruciate depression on
the right. Each half of the figure includes: on
the right, photographic samples of responses recorded
in response to stimulation of the contralateral ampullar
nerve; on the left, a diagram of the descent in tissue
section, with the sites where a response may be recorded
being indicated by a circle. The lateral plane (L) and
the height (H) of the terminal point of descent are given
in each diagram. The time (in msec) and amplitude (in
μV) calibrations given on one photographic sample in each
column are valid for all the photographic examples in
the same column.

II. Microphysiological Results

It appeared necessary to perform a unit study to attempt to
analyze the nature of these two projections to the contralateral
cortex upon vestibular stimulation. The sample of neurons col-
lected may be divided into three groups: 1) an initial group of

41 neurons recorded in the cortex bordering on the two banks of
the anterior suprasylvian sulcus; (2) a second group of 29 neurons
recorded in the cortex of the postcruciate depression; (3) finally,
a third group of 57 neurons recorded in depth in the fold formed
by the sulcus cruris on the mesial face of the cerebral hemisphere.

These neurons were studied from the standpoint of vestibular
and somatic afferents; those neurons with the least response to
one of these two types of stimulation were retained. For the
neurons responding to somatic stimulation, a simplified classi-
fication was used, at least at this stage of our analysis:
neurons with localized afferents, that is, those receiving somatic
afferents limited to a single member (generally contralateral)
were distinguished from neurons with convergent afferents, that
is, those activated by somatic stimulation of more than one
member.

I. Group of Neurons Recorded in the Suprasylvian Area

This group was characterized by the importance of the vestibu-
lar afferents: 42% of the neurons recorded in this cortical area
responded to stimulation of the ampullar nerve. These responses
occurred after an average latency period of 16.7 msec (±11.25).
It should be added, however, that histograms of the latency period
of these responses were in bimodal form. Thus a certain number   /67
of neurons responded to labyrinthine stimulation after a latency
period much shorter than 16.7 msec, and in some cases, even as
short as 4 msec.

Another important fact which should be pointed out: the
group of neurons responding after a brief latency period included
a small group (10% of the total population) receiving only
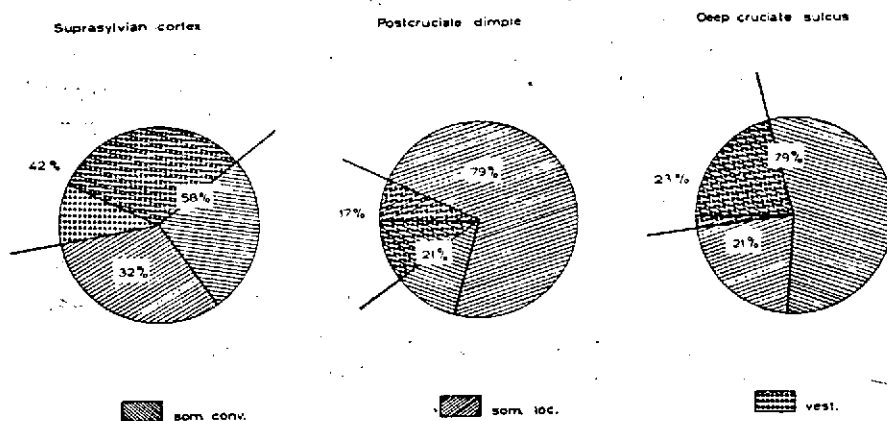vestibular afferents.

Suprasylvian cortex   Postcruciate dimple   Deep cruciate sulcus

som. conv.   som. loc.   vest.

Fig. 3. Diagramatic representation of the three groups of neurons studied. Left: group of neurons recorded in the suprasylvian cortex: n = 41. Center: group of neurons recorded in the postcruciate dimple: n = 29. Right: group of neurons recorded in the deep cruciate sulcus: n = 57. Striated area in upper right: total neurons receiving somatic afferents with a single member (som. loc.). Striated area in upper left: total neurons receiving somatic afferents with several members (som. conv.). Dotted area: total neurons receiving vestibular afferents (vest.). The numbers within the circles pertain to the striated areas; the numbers outside the circles pertain to the proportion of dotted area.

In regard to the somatic afferents within this sample, we should first emphasize the relatively high proportion (58%) of neurons receiving convergent somatic afferents, in comparison to the percentage (32%) of neurons activated by localized somatic afferents. An examination of histograms of the periods of latency in response to stimulation for each paw reveals a shorter latency period for the forepaws than for the hind paws (14.2 /69 msec and 17.91 msec for AC and AI and 25 and 27.53 msec for PC and PI, respectively). This may be explained by the fact that the recordings were performed around the suprasylvian sulcus, an area which corresponds, at least in part, to the second somatic region, whose somatotopic nature is well known (Figs. 3 and 4).
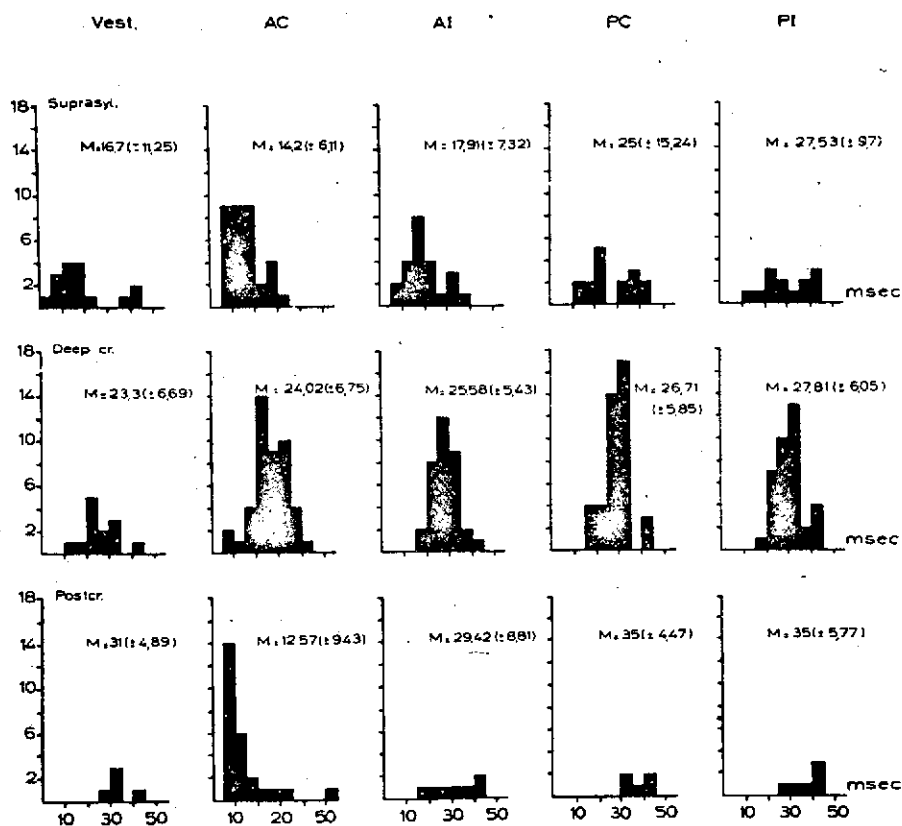
Fig. 4. Histograms of latency of unit sensory responses recorded; for the upper row, in the suprasylvian cortex (suprasyl.); center, in the deep cruciate sulcus (deep cr.); bottom row, in the postcruciate dimple (postcr.). The first column deals with responses produced by vestibular stimulation; the second, third, fourth and fifth columns resepectively pertain to responses produced by stimulation of the contralateral anterior paw (AC), ipsilateral anterior paw (AI), contralaterial posterior paw (PC) and ipsilateral posterior paw (PI). The abscissa of each histogram represents the latency of response expressed in milliseconds, and the ordinate, the number of neurons responding to the stimulation under consideration. The average latency period of the responses and the variants are given in the upper right of each figure. To be noted: 1) with reference to the vestibular responses, a shorter average latency period for the responses recorded in the suprasylvian cortex than for the responses recorded in the two other cortical sites; 2) with reference to the somatic responses, the large number of responses to stimulation of the contralateral anterior paw and the brief average latency period of these responses in the postcruciate dimple, that is, the primary somatic area; 3) the short average latency periods of the responses produced by stimulation of the anterior paws and recorded in the suprasylvian cortex where part of the second somatic area is located.

2. Group of Neurons Recorded in the Postcruciate Dimple

With regard to vestibular afferents, a relatively small pro-
portion of the neurons in this group (17%) were activated by
labyrinthine stimulation, and the average latency period of the
responses produced by this stimulation was long: 31 msec.

As for the somatic afferents, we primarily observed localized
somatic responses of primary type produced by stimulation of the
contralateral anterior paw. These responses were observed in 79%
of the neurons recorded and possessed a latency period of
12.57 msec, which is much shorter than the latency period of the
responses produced by stimulation of the other paws (29.42 msec
for AI and 35 msec for PC and PI). These results fall into line
with the cortical topical organization of the somatic afferents,
since these neurons were recorded fairly far to one side of the
primary somatic area, where the area of projection of the contra-
lateral anterior paw is located (Figs. 3 and 4).

3. Group of Neurons Recorded in the Deep Cruciate Sulcus

The unit vestibular responses recorded in this cortical area
did not appear to be any different from the vestibular responses
observed in the preceding group. The frequency of occurrence of
these responses was equivalent in both groups; they occurred in
23% of the neurons studied. The average latency period of these
responses (23.3 msec) showed no significant difference from the   /70
average latency period reported for the other group (group 2).

With regard to the convergent somatic responses (79%, as
opposed to 21% of localized somatic responses), an examination
of histograms of the latency periods revealed no difference be-
tween the responses to stimulation of each paw, and the average
latency periods obtained for each category of response were found

to be equivalent (AC = 24.00 msec; AI = 25.58 msec; PC = 26.71 msec; PI = 27.81 msec) (Figs. 3 and 4).

The effects of conditioning vestibular stimulation (producing no neuronal discharge) on the response of the vestibular nerve to somatic stimulation were studied in a few neurons from the three groups considered. It was thus possible to observe an inhibiting effect on the conditioning stimulation in one-third of the cases where this interaction was produced; this effect occurred after a latency period of 10 msec and continued for as long as 300 msec.

Before concluding this description of the results, we would once again like to draw attention to the following finding: the large majority of vestibular responses were found in neurons already receiving widely convergent afferents from the entire somatic periphery, without any detectable systematization, in comparison to the afferents arising from a hemicorpus. Thus was observed in the three groups considered; however, the vestibular area possesses an appreciable quantity of neurons which are activated only by vestibular stimulation. In this case, the unit response occurs after a relatively short latency period. The sum total of these properties give reason to assume that these vestibular afferents are primary in nature.

In conclusion: (1) our results obtained with concentric bipolar macroelectrodes do not support the theory of a short-latency period surface vestibular projection, even in the post-cruciate dimple -- area 3a, according to the cytoarchitectonic criteria of Hassler and Muhs-Clement [12] -- but they do reveal a distinct and very localized site of relatively early vestibular response in the deep cruciate sulcus (area 6).

2) Our extracellular unit recording method obviously limited the possibilities for analysis of vestibular cortical projections,

and did not permit deeper characterization of the vestibular
projection demonstrated at the level of area 6. Nevertheless, this
unit analysis underlines the primary nature of vestibular pro-
jection to the suprasylvian cortex and brings to light the abun-
dance of converging vestibulosomatic fibers in the neurons
of the cortical areas studied.

Discussion

This discussion will first be concerned with the specific
vestibular nature of the responses recorded in the deep cruciate
sulcus, and second, the large proportion of converging vestibulo-
somatic fibers in the three regions studied and the type of
somatic afferents which converge with the vestibular afferents.

The existence in the cat of an area of primary vestibular pro-
jection to the cortical surface has been well established since
the research of Andersson and Gernandt [1]. By means of their
specific technique of electrical stimulation of each branch of the
vestibular nerve, these investigators were able to localize this
projection on the cortex bordering on the anterior suprasylvian
sulcus. However, to our knowledge there has so far been no sys-
tematic microphysiological study in this area. The work we have
undertaken on this problem demonstrates the specific nature of
this region with regard to vestibular afferents and confirms the
large proportion of somatic sensory afferents at this level.
However, one point in the problem of cortical vestibular afferents
still needed to be clarified: vestibular projections to other
areas of the cortex. According to a large number of previous
studies on the anesthetized [20, 19] and unanesthetized [14, 15, 10]
cat, the motor cortex appears to be very rich in vestibular
afferents. The first part of this study underlines the specific
nature of vestibular projection to the motor cortex in an area
corresponding to cytoarchitectonic area 6. The stimulation used

(electric shocks delivered to the ampullar nerve emanating from the horizontal semicircular canal), the recording method with concentric bipolar macroelectrodes, the extremely precise locali- zation of the recording zone (anterior planes 23 to 24, lateral planes 4 to 8), the extremely low stimulation threshold producing a response (similar to the threshold observed in testing in the primary vestibular nuclei), as well as the relatively short latency period for the response are all elements which permit the assumption that the characteristic and specific projection of vestibular afferents to the motor cortex is involved. Furthermore, /72 it is interesting to compare these results to those obtained by Hassler [11], which show that stimulation of this cortical area -- area 6 aδ, in the nomenclature given by Hassler and Muhs- Clement [12] -- produces movements of the head and eyes in the horizontal plane. In addition, the research of Gildenberg and Hassler [7] shows that stimulation of this same cortical area produces responses in the neurons of the primary vestibular nuclei. Finally, work performed on the monkey by Fredrickson et al. [5] has also shown a zone of vestibular projection to the motor area. The investigators report that the responses obtained in this area have a lower amplitude, but that their latency period is identical to the responses recorded in the primary vestibular area. The existence of vestibular afferents in the motor cortex permits the assumption that these fibers use this information in executing the movements induced by the motor cortex.

Regarding the unit results obtained in the motor cortex, we would like to comment briefly on the results obtained at a deep level, that is, in the same area where we will record a macro- potential in response to vestibular stimulation. The neuron sample collected in this cortical area is similar from a vestibular standpoint to the neuron sample collected on the surface of area 3a. In both samples, a similar proportion of neurons acti- vated by vestibular stimulation was obtained, and the latency

periods observed were equivalent. In view of these results, there does not seem to be any significant difference between the two populations. With these extracellular recordings it was not possible to observe responses with a latency period similar to the latency period of the macroresponse recorded in area 6. Nevertheless, the very limited area where this response can be observed and the recording method using a concentric bipolar macroelectrode indicate that this wave is probably specifically vestibular in nature; it may reflect the presence of subliminal activity or inhibiting phenomena. This assumption is supported by the fact that we have observed the inhibiting effects of conditioning vestibular stimulation on a somatic response in several neurons, even though conditioning stimulation alone produced no response.

It seemed of value to point out the large number of converging vestibular and somatic afferents in our three recording sites. Aside from a small group of neurons in the primary vestibular area which received only vestibular afferents, all the vestibular responses were recorded from neurons already receiving somatic afferents which, in the large majority of cases, were emanating from wide peripheral fields. Several studies have already pointed out the considerable extent of the convergence of somatic and vestibular information in the cortex. In 1952, Mickle and Ades [21], using the technique of triggered potentials, demonstrated the richness of somatic information in the vestibular area of the cat. More recently, in-depth unit studies of the organization of the somatic afferents in the vestibular area, made by Landgren et al. [12] and by Silfvenius [29], have shown that the neurons in this area of the cortex receive somatic afferents from cutaneous and articular muscular receptors. The present study, using both stimulation of an ampullar nerve and of cutaneous areas located at the level of the various members, reveals the convergence of vestibular and somatic influxes at a single cortical neuron. A similar study, but one in which the vestibular

stimulation consisted of polarization, has been undertaken in the monkey by Schwarz and Fredrickson [28], permitting these investigators to conclude that the vestibular area is an area of bimodal primary projection. However, these convergences are not characteristic of the cortical stage, but may already be found in the primary vestibular nuclei, as has been demonstrated by Fredrickson et al. [6] in the cat, using the polarization techniques. In the thalamus of the cat, Sans et al. [27] have revealed two sites of response to stimulation of the ampullar nerve: (1) an initial site of short latency period response located in the dorsomedian part of the VPL and the ventral part of the VL; (2) a second site of responses with a longer latency period located in the median part of the VL. As for the possible convergence of somatic and vestibular afferents, these investigators were able to observe this phenomenon in some neurons recorded in the innermost part of the VLP.

In our experiments, the somatic stimulation consisted of electric shocks delivered to the paws. So far it has not been possible for us to state, on the basis of our results, what types of somatic afferents (muscular, cutaneous or articular) converge with the vestibular afferents. Partial answers may be found in the research of Fredrickson et al. [6] on the cat and that of /74 Schwarz and Fredrickson [28] on the monkey. During their experiments, in which the vestibular stimulation consisted of polarization of the labyrinth, these investigators demonstrated the convergence of vestibular and somatic influxes emanating from nearby neck joints in the vestibular nuclei [6], while in the motor cortex [28], they observed the convergence of vestibular and somatic influxes from articular receptors and muscular receptors. Thus this would basically be a convergence of vestibular afferents and proprioceptive afferents. In addition, it should be noted, as pointed out by Sans [26], that in the cat cortex, all the sensory afferents which play a role in the regulation of muscular tonicity and posture converge to the same areas.

Summary

The projection of vestibular afferent fibers to the posterior region of the motor cortex (that is, the postcruciate dimple) and to the primary vestibular area is studied comparatively.

Experiments have been performed on chloralosed cats immobilized with curare and given artificial respiration. The responses triggered in the anterior suprasylvian area and the postcruciate dimple by electrical stimulation of the nerve emanating from the ampulla of the horizontal semicircular canal have been recorded by surface monopolar recording, deep recording using concentric bipolar macroelectrodes, and unit recording using glass micropipettes.

The results obtained with the macroelectrodes do not support the theory of a short latency vestibular projection on the surface of the postcruciate dimple, but do reveal a distinct and very localized site of relatively early vestibular response in the deep cruciate sulcus. Unit recordings were made in the following three sites: the primary vestibular area, the postcruciate dimple and the deep cruciate sulcus.

The primary nature of the vestibular projection to the suprasylvian cortex is pointed out. In addition, the richness of vestibulosomatic convergence in the cortical areas studied is /75 revealed, since in the three neuron groups considered, the large majority of vestibular responses was obtained from neurons already receiving somatic afferents from widespread areas.

Acknowledgements

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